

Availability and species diversity of forest products in a Neotropical rainforest landscape



Armando Navarrete-Segueda^a, Miguel Martínez-Ramos^{b,*}, Guillermo Ibarra-Manríquez^b, Jorge Cortés-Flores^b, Lorenzo Vázquez-Selem^c, Christina Siebe^a

^a Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Circuito de la Investigación Científica, Circuito Interior, Delegación Coyoacán, Ciudad de México CP 04510, Mexico

^b Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Antigua carretera a Pátzcuaro No. 8701, Col. San José de la Huerta, CP 58190 Morelia, Michoacán, Mexico

^c Laboratorio Nacional de Análisis y Síntesis Ecológica, Escuela Nacional de Estudios Superiores, Unidad Morelia, Universidad Nacional Autónoma de México, Antigua Carretera a Pátzcuaro No. 8701, Col. San José de la Huerta, CP 58190 Morelia, Michoacán, Mexico

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ABSTRACT

Tropical rainforests harbor a high diversity of tree species, offering a potentially rich array of timber (TFP) and non-timber (NTFP) forest products. The supply of such products has been commonly evaluated at the local (plot) scale; however, little is known about how their availability and diversity change at the landscape scale, particularly in heterogeneous environments. This information is critical in designing landscape forest management programs. Here, we assess the extent to which the frequency, abundance, diversity, composition and productivity (aboveground biomass) of tree assemblages with potential forest products (PFPs) change across three landscape units (LUs) that differ in soil and topographic conditions. The study was carried out in a well-conserved old-growth tropical rainforest in southeastern Mexico. Three plots (0.5 ha each) were established per LU, in which all trees ≥ 10 cm were inventoried, taxonomically identified and assigned to eight forest product categories. General linear models, multiple regression and ordination analysis (CCA) were used to assess structural and compositional changes in the tree assemblages supplying different PFPs among LUs and along soil physicochemical gradients. More than half (94 species, 57%) of the total number of identified species (165) had one or more PFPs, mostly related to timber products. Ordination analysis showed that the abundance of species with different PFPs has a heterogeneous distribution among LUs, mostly related to changes in soil nitrogen, pH and aluminum saturation. Variation among LUs in terms of tree biomass was strongly driven by soil available phosphorus and soil physiological depth. Each LU had a different potential to provide forest products, producing a diverse mosaic of PFPs within the landscape. Decisions concerning sustainable forest management should consider such variability in the availability and diversity of forest products across landscapes, as well as the environmental factors that govern this spatial variation.

1. Introduction

Tropical rain forests (TRF) are mega-diverse ecosystems that supply a wide array of goods and benefits for human well-being (de Groot et al., 2012). Among such goods are the timber (TFP) and non-timber (NTFP) forest products. The latter includes any biotic resource that does not imply the logging of trees, such as edible fruits, fuelwood, materials for construction (e.g. roofing leaves), as well as ornamental and medicinal plants (Belcher, 2003; de Groot et al., 2010). Considering the classification of ecosystem services established by MEA (2005), forest

products are an important provision ecosystem service that adds to the other support, regulation and cultural services supplied by TRF (Daily, 1997).

In the Anthropocene, global demand for food and expansion of agriculture has driven severe deforestation in tropical regions (Gibbs et al., 2010). Deforestation has produced a critical reduction of global biodiversity and the loss of ecosystem services of local, regional and global importance (Foley et al., 2011). Satisfying the present and future demand for food, without compromising the biodiversity and ecosystem services of TRF, is therefore vital for the sustainable management of

* Corresponding author.

E-mail addresses: anavarretesegueda@yahoo.com.mx (A. Navarrete-Segueda), mmartinez@cieco.unam.mx (M. Martínez-Ramos), gibarra@cieco.unam.mx (G. Ibarra-Manríquez), jcortes@cieco.unam.mx (J. Cortés-Flores), lselem@igg.unam.mx (L. Vázquez-Selem), siebe@unam.mx (C. Siebe).

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these forest ecosystems (Harvey et al., 2008). Sound management of forest products requires an assessment of their availability and diversity, as has been conducted in some tropical forests (e.g. Dattagupta et al., 2014; Ibarra-Manríquez et al., 1997; Peters et al., 1989). Some studies have shown a positive relationship between plant species diversity and the number of potential forest products at plot level (e.g. Quijas et al., 2010). There are studies that address the landscape-scale variation of tropical forest products and their relevance to forest management (e.g. Newton et al., 2012; Salo and Toivonen, 2009; ter Steege et al., 2002). However, most studies focused separately on timber or non-timber products. Therefore, there is a need of studies assessing changes in the availability, diversity and composition of forest products at landscape scales considering both forest product types. This approach is important for designing management strategies of forest products in an integral way, especially in areas with high environmental heterogeneity.

The extraordinary tree species diversity in TRF is a result of the fact that most species have low population densities, which in turn causes a low availability of species-specific forest products. Since the population density and spatial distribution of species supplying forest products can affect harvesting quotas at the local and landscape scales, documenting these demographic attributes should help with the design of appropriate sustainable management programs for TRF products (Fortini et al., 2006; Newton et al., 2012; Ribeiro et al., 2014; Ticktin, 2004). Sustainable TRF management also addresses the biological and environmental complexity of these forest ecosystems (Ros-Tonen, 2000). For example, most TRF tree species require specific resources (e.g. quantity and quality of light, availability of soil nutrients and water), conditions (temperature, humidity) and biotic interactions (mutualistic associations with animals, bacteria and fungi) in order to germinate, establish, grow and reproduce (Gravel et al., 2011; Wright, 2002). Sustainable forest management therefore not only requires basic information about the availability and diversity of forest products but also about the ecological factors that determine the spatial variation of these attributes (Guariguata et al., 2010).

Several studies have documented important levels of tree species turnover associated with environmental heterogeneity in TRF landscapes (e.g. Baldeck et al., 2013; Condit et al., 2013; John et al., 2007; Phillips et al., 2003; Toledo et al., 2012). Soil nutrient content (Baldeck et al., 2013; John et al., 2007; Phillips et al., 2003; Swaine, 1996) and soil water retention capacity (Sollins, 1998) have been identified as important variables affecting tree species distribution and species turnover. Soil variables could therefore also play an important role in determining spatial variation in the availability and diversity of potential forest products (PFPs). It is possible to map spatial changes in soil nutrient content and water availability using topographic variation, since topography affects soil water availability and the biogeochemical processes that influence soil nutrient availability (Baldeck et al., 2013; Brown et al., 2013). Topographic and soil variables can be integrated within discrete, relatively homogenous, LUs, through a process of geopedological delimitation (Zinck et al., 2016). When LUs are recognized, it is possible to evaluate the effect of soil variables on the spatial distribution and population density of plant species (Phillips et al., 2003). This, in turn, helps to identify soil and topographic factors that influence the potential spatial availability of forest products. This potential availability can be assessed through the abundance (trees per unit area), frequency of occurrence, and aboveground biomass (AGB, hereafter referred to as “biomass”) of the tree species that provide the PFPs. Abundance and frequency give an idea of the spatial attainability of the forest products while biomass reflects the potential productivity of tree species (Clark et al., 2001).

The Lacandon forest in southeast Mexico is one of the largest tropical rainforests of Mesoamerica; it is broadly representative of the TRF of southern Mexico and Central America (de Jong et al., 2000; Meli and Carabias, 2015). It has a high species diversity [120 plant species in 0.1 ha (Dirzo et al., 2009) and more than 200 tree species with stems

≥ 10 cm DBH in 7 ha (Martínez-Ramos, 2006)], which is related to its edaphic and topographic heterogeneity (Siebe et al., 1995). The historical cover of the Lacandon forest has decreased by 66% over the last four decades as a result of conversion of the land to agriculture (Meli and Carabias, 2015; Zermeño-Hernández et al., 2015) and the Mexican government has decreed part of the forest (331,200 ha) as the UNESCO Montes Azules Biosphere Reserve (MABR) in 1978. This reserve aims to preserve the biodiversity and ecosystem functions and services of old growth forest ecosystems, limiting any extractivism or other human activity. In the area surrounding the MABR, where same forest topographic and soil formations exist (Martínez-Ramos, 2006; Navarrete-Segueda et al., 2015) (Appendix A, supplementary material), governmental programs involving ecotourism and payment for environmental services have been conceived as part of the sustainable management of human modified landscapes (HMLs). However, accelerated demographic growth and human activities cause intense pressure, on remaining forest fragments surrounding MABR landscapes (Carabias et al., 2015). An ecological analysis of the availability and distribution of forest products that considers environmental heterogeneity is urgently required in such HMLs.

In this paper, we assess changes in the abundance, frequency, biomass, diversity and composition of tree assemblages that supply PFPs across LUs that contrast in terms of soil and topographic characteristics, in the Lacandon tropical rainforest. We use areas of the MABR as a study system in an attempt to provide an ecological basis for the extractivism potential and management of forest products in HMLs. The objectives of the study were to: i) evaluate the potential availability (abundance, frequency and biomass) and diversity of forest products supplied by tree assemblages present in an environmentally heterogeneous landscape, ii) document the variation in such potential within and among types of LU, and iii) assess the extent to which such changes are associated with variation in the soil (water and nutrient availability) and topographic attributes of the landscape.

2. Methods

2.1. Study site

This study was conducted in the Montes Azules Biosphere Reserve (16°04'N and 90°45'W), located in the region of the Lacandon tropical rainforest, in Southeastern Mexico. Total annual precipitation in this area is ca. 3000 mm and mean annual temperature is 22 °C; there is a short dry season from February to April, with less than 60 mm of precipitation per month (Martínez-Ramos et al., 2009). The composition, structure and diversity of the forest are influenced by variation in the geology, soils and topography (Ibarra-Manríquez and Martínez-Ramos, 2002; Siebe et al., 1995).

The geology of the region comprises sedimentary rocks affected by folding and fracturing, such that outcrops of limestone, claystone and sandstone, as well as conglomerates, are structured in systematic patterns. Limestone outcrops occur on mountain ranges covering an altitudinal gradient of 150–700 m, affected by a karstification process. Low-hill areas occupy the depressions between karst-ranges in which claystone, sandstone and conglomerate outcrops alternate (García-Gil and Lugo-Hupb, 1992). Landscape units can be identified within this complex geological system, based on lithology, topography and soil properties (Siebe et al., 1995). The density and distribution of plant species respond to these contrasting landscape attributes (Ibarra-Manríquez and Martínez-Ramos, 2002; Martínez-Ramos, 2006).

2.2. Landscape units

Landscape units (LUs) were characterized based on the hierarchical geopedological classification system proposed by Zinck et al. (2016). These units were delimited by visual interpretation of the external characteristics of landforms in aerial photographs at scale 1:20,000 and

Table 1

Topographic and soil attributes of three contrasting landscape units (LUs) in the Lacandon forest, southeastern Mexico. Mean values and standard error (SE) are shown for the soil properties of three sampling sites per LU in the *solum*. For each attribute, values with a different superscript letter differ statistically (ANOVA and Tukey post hoc test $P < 0.05$).

| LU characteristics | Fluvial terrace | Low hill | Karst range |
|--|---------------------------|-------------------------|--------------------------|
| Slope (°) | 0–2 | 2–26 | 18–26 |
| Surface stoniness (%) | 0 | 0 | 40 |
| Soil Nitrogen (t ha ⁻¹) | 12.2 ± 3.0 ^a | 4.8 ± 0.5 ^a | 10.3 ± 2.0 ^a |
| Plant available phosphorous (mg kg ⁻¹) | 9.2 ± 1.9 ^a | 6.4 ± 3.2 ^a | 11.1 ± 5.7 ^a |
| Aluminum saturation in the cation exchange complex (%) | 2.1 ± 2.0 ^b | 22.6 ± 1.9 ^a | 0 ^b |
| pH | 5.4 ± 0.3 ^b | 4.1 ± 0.1 ^a | 6.1 ± 0.2 ^b |
| Physiological depth (dm) | 13.4 ± 0.9 ^b | 1.2 ± 3.5 ^a | 4.93 ± 1.7 ^a |
| Soil available water-holding capacity | 161.4 ± 16.7 ^b | 34.6 ± 3.8 ^a | 37.1 ± 14.4 ^a |

using a digital elevation model (DEM). Geological (SGM, 1997) and soil (Celedón, 2006; Siebe et al., 1995) data were also considered. Three contrasting LUs were selected according to lithology, soils and topography. The most distinctive characteristics of these LUs are presented in Table 1.

In each LU, three 20 × 250 m (0.5 ha) plots were established, covering a total sampled area of 4.5 ha. A soil profile was described in each plot (three profiles per LU) and intact soil cores were taken in order to determine bulk density. In each profile, soil samples were collected from each genetic horizon [a layer of soil, approximately parallel to the soil surface, with properties (e.g. texture, bulk density) and characteristics (e.g. thickness, amount of root tissues) that distinguish it from the layers immediately above or below (Brady and Weil, 1996)] for subsequent laboratory analysis in order to obtain a precise estimate of the soil nutrient content (Ellert and Bettany, 1995). In this way, the morphogenetic variation of the soils and its effect on the soil nutrient reserves of the different LUs was assessed. Soil physicochemical analyses (total carbon, total nitrogen, available phosphorus, exchangeable cations, pH, Al³⁺ and H⁺, bulk density and soil particle size distribution) were conducted in the laboratory following standard procedures (Schlichting et al., 1995; Van Reeuwijk, 1992) on dry soil samples sieved to < 2 mm.

2.3.1. Estimates of the soil nutrient availability

One of the main difficulties with comparing studies of the effect of soil nutrient availability on tree diversity is that soil nutrient concentrations are often measured using different techniques, which can complicate direct comparison of the results among studies (Clinebell II et al., 1995). Furthermore, simple comparison of nutrient concentrations does not take into account the fact that the soil nutrient pool depends on the mass of soil under consideration (Ellert and Bettany, 1995). For this reason, the concentrations of the elements determined in each genetic horizon within the *solum* (i.e. the A and B horizons, which represents the most biologically active zone of the soil, and where most roots and plants grow) were multiplied by the bulk density (quantified in the laboratory) and corrected for the stoniness and thickness of each horizon estimated in the field. Plant-available water holding capacity, physiological depth, field capacity and aeration capacity of the *solum* were estimated based on Siebe et al. (1996) and using data pertaining to soil texture, soil organic matter content and bulk density.

2.4. Tree sampling and characterization of PFPs

In each of the nine 20 × 250 m (0.5 ha) plots described above, all trees with a diameter at breast height (DBH) ≥ 10 cm were recorded, identified to species level, and measured in DBH. In the literature, we

identified PFPs reported for each recorded tree species; the PFPs were classified in the following categories (Appendix B, see supplementary material): fodder, food, fuelwood, medicinal, melliferous, ornamental, plywood-paper pulp and timber. Aboveground biomass of each tree was estimated using the allometric equation provided by Chave et al. (2014). This equation considers DBH and species-specific wood density values, which were obtained from a previously published study (Poorter et al., 2015). The biomass values of all trees with PFPs recorded in each plot were summed per species.

2.5. Data analysis

Using data pertaining to the species with PFPs, we obtained mean (± s.e.) values of density (number of trees ha⁻¹), biomass (Mg ha⁻¹), species richness (number of species in 0.5 ha), species diversity (H', Shannon index in 0.5 ha) and evenness (J, Shannon index in 0.5 ha). For each LU, H' and J were calculated as indicated in Magurran (2013). Furthermore, we quantified the relative frequency of occurrence of each species across the nine study plots and the three LUs.

To assess differences in the availability (tree density and biomass) and diversity (species richness, H' and J) of tree assemblages with PFPs among the LUs, we performed general linear models. For count variables (density and species richness), we used a Poisson error and log-link function, while for continuous variables (biomass, H' and J), we used a normal error and identical link function. These models were also used to assess differences in species richness, density and biomass among the tree assemblages that supplied different PFPs, as well as to assess differences among LUs in these three assemblage attributes for each PFP. We also used a Chi-Square test to assess differences among LUs in terms of the frequency of species with 1, 2, 3 or more different PFPs.

To assess changes in dominant species among the LUs, we constructed species-rank curves for each individual LU (lumping species data of the three plots per LU) and for all of the LUs combined (lumping data from all nine study plots). The curves were constructed following Magurran (2013), and considering separately the abundance and biomass of tree species with PFPs. We performed this analysis using the 'BiodiversityR' (Kindt and Coe, 2005) package of R (R Core Team, 2015). We used canonical correspondence analysis (CCA) to test differences in species composition among LUs and associations between species distribution and the soil properties (Palmer, 1993). In this analysis, we used species abundance and orthogonal soil variables, which are indicators of nutrient pools and water availability. Finally, we used a multiple linear regression analysis to assess changes in species biomass associated with gradients of soil physicochemical properties in the landscape. These analyses were conducted with the 'vegan' package (Oksanen et al., 2015) of R (R Core Team, 2015).

3. Results

3.1. Overall availability, diversity and species composition of trees with PFPs

In total, 165 tree species were recorded across all of the studied plots, of which 57% (94 species) had PFPs (Appendix B, see supplementary material). Forty-one species (44% of the total species with PFPs) had only one PFP, 20 species had two (21%), 13 species had three (14%), 11 species had four (12%), 7 species had five (7%) and 2 species had six (2%). *Alchornea latifolia* (Euphorbiaceae) and *Bursera simaruba* (Burseraceae) were the species that provided the highest number of forest products (6), while *Ampelocera hottlei* (Ulmaceae), *Brosimum alicastrum* (Moraceae), *Ceiba pentandra* (Malvaceae), *Dendropanax arboreus* (Araliaceae), *Luehea candida* (Malvaceae), *Manilkara zapota* (Sapotaceae) and *Pouteria sapota* (Sapotaceae) had five products. *Dialium guianense* (Fabaceae), *Guarea glabra* (Meliaceae), *B. alicastrum*, *Pouteria durlandii* (Sapotaceae) presented a wide spatial distribution

Table 2

Change in structural variables [mean and standard error (SE)] of tree assemblages supplying PFPs among landscape units (FT = fluvial terrace; KR = Karst range; LH = low hill), in the Lacandon tropical rainforest, southeastern Mexico. Values with a different superscript letter differ statistically (GLM, $P \leq 0.05$).

| | Fluvial terrace | Karst range | Low hill |
|--|---------------------------|---------------------------|---------------------------|
| Abundance (trees ha ⁻¹) | 241 ± 15 ^b | 174 ± 17 ^a | 298 ± 48 ^c |
| Aboveground biomass (Mg ha ⁻¹) | 282.0 ± 40.9 ^b | 139.0 ± 11.4 ^a | 124.0 ± 13.4 ^a |
| Species richness (species in 0.5 ha) | 33.0 ± 2.4 ^b | 27.0 ± 0.6 ^a | 38.0 ± 3.7 ^b |
| Species diversity (H') | 1.08 ± 0.05 ^b | 0.76 ± 0.08 ^a | 1.05 ± 0.05 ^b |
| Evenness (J) | 0.71 ± 0.03 ^b | 0.53 ± 0.06 ^a | 0.67 ± 0.01 ^{ab} |

(recorded in 89% of the plots), while most of the species (44% of 94 species) had a narrow distribution (< 25%, [Appendix B, supplementary material](#)).

On average (\pm s.e.), a hectare of forest had 238 ± 24 trees with PFPs, representing a biomass of 181.8 ± 28.3 Mg/ha, a species richness of 33 ± 2 species per 0.5 ha, and a species diversity (H') of 0.96 ± 0.06 in 0.5 ha (Table 2). Most species are used for timber (59, 63% of the total species with PFPs). The trees used for timber were more diverse (Fig. 1A) and had higher density (Fig. 1B) and biomass (Fig. 1C) than those with different NTFPs. Interestingly, 57% of the timber species also supply NTFPs. The number of tree species with NTFPs per plot varied between 3 and 15 (Fig. 1A) and, considering all of the study plots together (4.5 ha), the NTFPs included those of medicinal (42 species, 45% of total species with potential PFPs), food (33, 35%), fuelwood (29, 31%), melliferous (12, 13%), ornamental (12, 13%) and fodder (7, 7%) use. Trees with medicinal, food and fuelwood products also exhibited high density and biomass (Fig. 1B and C).

3.2. Change of availability and diversity of PFPs among LUs

The frequency of species with different numbers of PFPs did not differ among the LUs ($X^2 = 2.13$, d.f. = 8, $P > 0.50$). Twenty-three percent of the 94 species with PFPs occurred in all three LUs, 38.3% in two, and 38.3% in just one. Overall, the tree assemblages with PFPs in the karst-range sites exhibited lower density, species richness, diversity and evenness than those on the fluvial terrace, especially those in the low-hill sites (Table 2). The fluvial terrace sites presented higher biomass than the other LUs.

In the low-hill sites, the tree assemblages supplying timber products had higher species richness (Fig. 1D) and density (Fig. 1E) than those in the other LUs, while tree assemblages supplying timber and medicinal products had higher biomass in the fluvial terrace than in the low-hill sites (Fig. 1F). Finally, in the karst-range sites, the species richness of tree assemblages with plywood was lower than in the fluvial terrace sites (Fig. 1D). For the other NTFPs, we found differences among LUs only in terms of assemblage density, and these differences varied depending on the particular NTFP considered (Fig. 1E).

Species-rank curves based on species abundance showed variation in the dominant species with PFPs among the LUs (Fig. 2): *Ampelocera hottlei*, *Dialium guianense* and *Guarea glabra* (Meliaceae) were the three most abundant species in the fluvial terrace sites, *B. alicastrum*, *M. zapota* and *Quararibea funebris* (Malvaceae) in the karst-range sites and *D. guianense* was the single dominant species in the low-hill sites. Combining all of the LUs, the three most abundant species with PFPs were *D. guianense*, *G. glabra* and *B. alicastrum*. Species-rank curves based on species biomass showed a different combination of dominant species in each LU (Fig. 3). The species with highest biomass in the fluvial terrace sites were *Licania platytypus* (Chrysobalanaceae), *B. alicastrum*, and *D. guianense*; at the karst-range sites, these were *B. alicastrum* and *M. zapota*, while *D. guianense* and *Terminalia amazonia* (Combretaceae) were the dominant species in the low-hill sites. Interestingly, *B. alicastrum*

appeared among the three species of highest biomass in all of the LUs, despite the fact that this species was less abundant than other dominant species in biomass. For example, in the fluvial terrace sites, this species did not appear among the ten species of highest abundance but was second in terms of biomass. Combining all of the LUs, *B. alicastrum*, *D. guianense* and *Spondias radlkoferi* (Anacardiaceae) were the top three dominant species in biomass.

The two main axes of the CCA ordination of tree species with PFPs explained 69% of the total variance among sites (Fig. 4). The species were clearly segregated among LUs, which shows that species composition differed among these units. The first axis was positively correlated with soil nitrogen content ($P < 0.05$), thereby separating species found in the karst-range sites (habitat with higher soil nitrogen and water drainage but lower soil rooting depth) from those found in the other LUs (Fig. 4, Table 1). The second axis was negatively correlated with aluminum saturation ($P < 0.05$) and separated the species in the low hills (higher aluminum saturation) from those in the fluvial terrace sites (higher soil rooting depth). Finally, multiple linear regression analysis including all study plots showed that the biomass of trees with PFPs was strongly and positively related to soil available phosphorus and physiological depth ($R^2 = 0.90$, $P < 0.01$).

4. Discussion

4.1. Overall availability and diversity of PFPs

Tropical rainforests are not only diverse in tree species but also rich in forest products, as documented in this study. Almost two thirds of the 165 tree species recorded in this study had at least one PFP. Because of study was restricted to trees with DBH ≥ 10 cm, we can expect this number would be higher if shrubs, small understory trees, lianas and epiphytes were included. The fact that most of these species could supply a single forest product is in line with findings reported by Ibarra-Manríquez et al. (1997) and Dattagupta et al. (2014) for other TRFs. More studies are required to verify whether the predominance of species supplying a single forest product constitutes a general pattern in TRFs. The fact that most tree species with PFPs were categorized as timber products parallels the results of Ibarra-Manríquez et al. (1997) for the TRF of Los Tuxtlas, Mexico. Among our timber species, a third were reported with more than two NTFPs, which coincide with figures reported by Herrero-Jáuregui et al. (2009, 2013) for other TRF localities.

Overall, our results show that the Lacandon TRF provides a rich set of NTFPs particularly for medicinal, food and fuel-wood uses (Fig. 1A–C). To reach sustainability, however, future studies will need to define sustainable harvesting thresholds based on the rate of resource production, the rate of resource harvesting, plant resilience to harvesting, ecosystem disturbances caused by harvesting, and economical-ecological harvesting trade-offs (e.g. Hernández-Barrios et al., 2015), as has been done for some timber (e.g. ter Steege et al., 2002; Zimmerman and Komros, 2012) and non-timber forest products (e.g. Gaoue, 2016; Gaoue et al., 2016; Ribeiro et al., 2014; Ticktin, 2005).

4.2. Change in availability and diversity of PFPs across the landscape

The fact that density, biomass and species diversity of trees supplying PFPs varied among LUs (Table 2) indicates important soil-topographic habitat effects on the performance and spatial distribution of species. Previous studies have shown that the spatial distribution and productivity of tropical tree species respond to variations in soil and topography in the landscape (Baldeck et al., 2013; Condit et al., 2013; Laurance et al., 2010, 1999; Phillips et al., 2003; Sollins, 1998). In our study area, spatial variation in tree species composition was explained by changes in soil nitrogen content, soil rooting depth and aluminum saturation (Fig. 4). The spatial variation in biomass was strongly and positively related to changes in soil available phosphorus and rooting

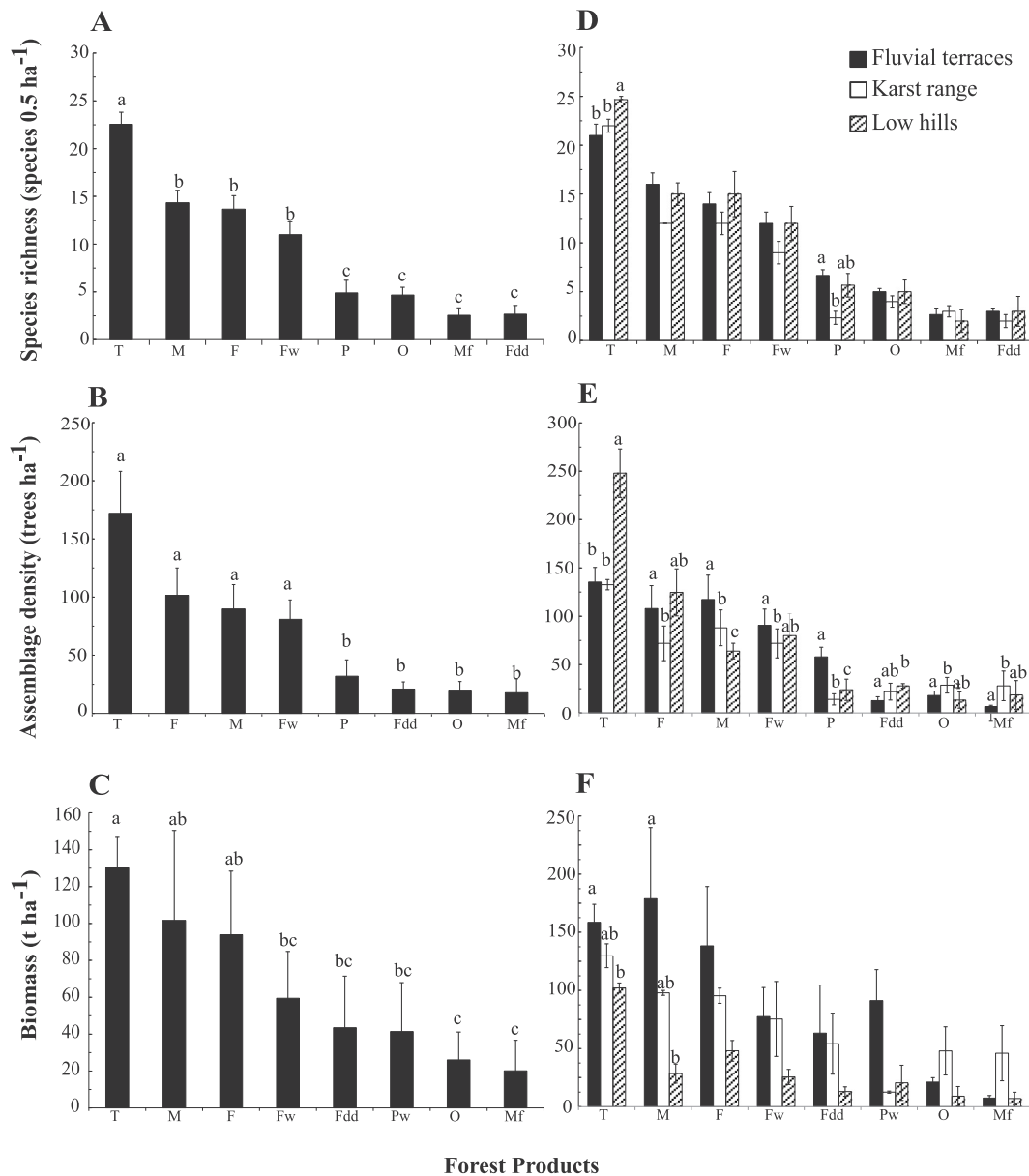


Fig. 1. Change in structural attributes (species richness, assemblage density, and above ground biomass) of tree assemblages with potential forest products (PFPs) in the Lacandon tropical rainforest, southeastern Mexico. T = timber; M = medicinal; F = food; Fdd = fodder; Fw = fuelwood; Pw = plywood; O = ornamental; Mf = melliferous. From A to C, mean \pm S.E. (vertical lines; n = 9 plots per PFP) values of the structural attributes of tree assemblages supplying each PFP are shown; bars with a different superscript letter indicate significant differences ($p < 0.05$, general linear model tests). From D to E, mean \pm S.E. values (n = 3 per LU) for each structural attribute, LU, and PFP are shown; bars with different superscript letters within each PFP differ significantly ($P < 0.05$).

depth. In the LU (Alluvial Terrace) that had a higher availability of soil nutrients and water, deeper soil and flatter terrain trees reach larger sizes, which in turn acts to reduce the space available for other trees. This produces tree assemblages of relatively low density and species diversity (Clark and Clark, 2000; Laurance et al., 1999). The lowest biomass of trees with PFPs at the Low Hill sites was probably due to the low levels of available phosphorus found in that LU, since this nutrient has been reported to limit tropical forest productivity (Laurance et al., 1999; Paoli et al., 2008; Vitousek, 1982). Low pH values and high aluminum saturation, as found in the Low Hill sites, cause phosphorus to be present in insoluble compounds, which are unavailable to the vegetation (Chapin et al., 2011).

Strong relationships between the spatial distribution of tropical forest species used for timber and soil properties have been well documented (e.g. Banin et al., 2014; Paoli et al., 2008), but not for species supplying NTFPs. Significance effects, particularly on tree

assemblage density, were noted when analyzing the effects of LUs on tree assemblages supplying specific NTFPs (Fig. 1E). These results support the notion that forest products and their availability are unequally distributed in the landscape (Campbell et al., 1997; Fortini et al., 2006). Establishing causal relationships between LU's environmental variability and the availability and diversity of NTFs is complicated because same species may supply two or more products (e.g. edible fruits and medicinal products). Furthermore, different species supplying the same product can respond differentially to environmental variation, which complicates the examination of the effects of environmental heterogeneity effects on the spatial variation of each NTFP. This may explain why most tree assemblages supplying different NTFPs did not differ among the studied LUs, in terms of biomass or species richness (Fig. 1D and F). Another challengeable issue is the difficulty of scaling the abundance and diversity of forest products recorded from a plot up to landscape level. Such difficulty emerges when beta species

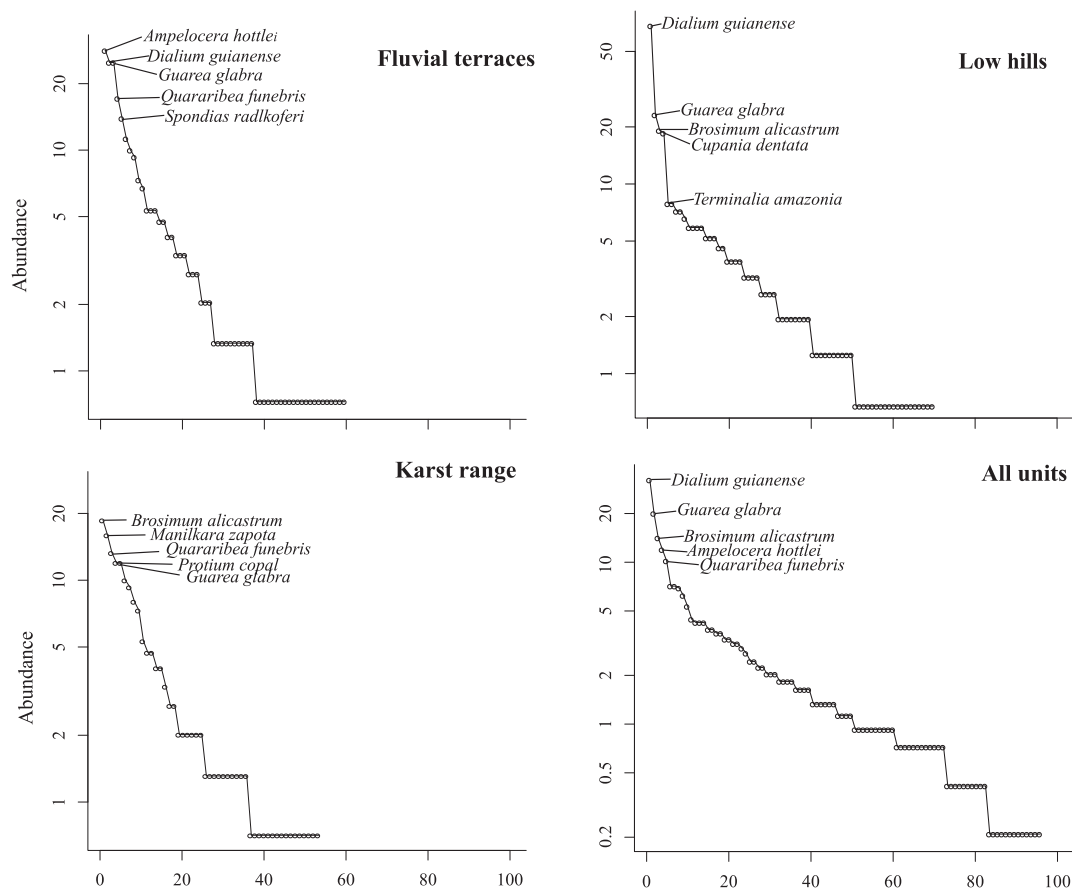


Fig. 2. Species-rank curves based on species abundance for tree assemblages supplying PFP in the Lacandon tropical rainforest, southeastern Mexico. The curves correspond to each of the three study landscape units (fluvial terraces, karst-range, and low hills) and to all sites combined (all units). On the X-axis, species are ranked in a decreasing order of abundance while on the Y-axis, the number of trees of each species per hectare is indicated.

diversity is high, as is commonly the case in tropical rainforests (e.g. Condit et al., 2002). As our CCA analysis showed, this is true for our study landscape, where a strong variation among LUs in composition of tree species supplying PFPs exists (Fig. 4). Such beta diversity also indicates that heterogeneous landscapes may provide a wide array of different forest products, because PFPs found in a given LU could be different in identity and quantity to those found in other LUs. This means that forest products present in different landscape units are complementary goods when considering all the landscape. It is therefore important to study the availability and diversity of forest products using sampling designs that encompass the environmental variability to which such beta diversity responds (Clark and Clark, 2000), as was sought in the present study.

4.3. Implications for management of multiple forestry products

Identifying key soil variables that influence the availability and diversity of PFPs in the landscape is an important step towards the development of sustainable forest management. However, there are other factors associated with human dimensions that should be considered when the goal is sustainable forest management (Panayotou and Ashton, 1992). One such factor is selectivity of the quality and quantity of the forest product for market demand (Arnold and Pérez, 2001). For example, in the case of edible fruits, the flavor and quantity of the pulp must be considered (Ibarra-Manríquez et al., 1997). For example, in our study forest there were several species of *Ficus* (Moraceae), abundant in the Fluvial Terrace, which produce edible fruits. However, these fruits are either very small (*F. pertusa*) or not sweet when large (*F. yoponensis*). Furthermore, despite being very edible, the fruits of *D. guianense*, the most abundant tree in the Low Hill sites, have

little pulp. In contrast, *M. zapota* produces fruits that are highly appreciated in the market for their flavor and rich pulp but its availability is limited to the Karst Range sites. Thus, despite the fact that several species provide a specific forest product, these can vary considerably in quality and quantity across the landscape (Sheil and Wunder, 2006). Another human-oriented factor is the variation that exist among local interests in terms of exploiting different resources of the same species; this produces conflicts in the use of such species (Guariguata et al., 2010; Herrero-Jáuregui et al., 2009). For example, *Diospyros nigra* (J.F.Gmel.) Perrier. (Ebenaceae), *B. alicastrum*, *M. zapota* and *P. sapota* are valuable species for their timber but are equally valuable for their very edible fruits (Appendix B, supplementary material). Thus it is vital to incorporate the priorities of local users (Sheil et al., 2006), as well as to identify market opportunities and provide market knowledge associated to commercialization of forest products (Guariguata et al., 2012). Otherwise, harvesting of species supplying multiple forest products, counted without adequate local consultation and organization, may alienate local stakeholders (Sheil et al., 2006) and create governance problems (Guariguata et al., 2010; Radachowsky et al., 2012), poverty and ecological degradation.

Multipurpose species management success is multifactorial and context-dependent (Guariguata et al., 2010). Independently of the main use choice for each species, management practice design should consider the spatial landscape variation in the attainability and availability of the selected species. In our study, some species were restricted to a particular LU or presented wide variation in abundance and biomass across LUs. Such changes in ecological attributes of the species therefore must be considered. Identifying the relationships between the change in the availability and diversity of forest products in the landscape and the environmental variation that causes such change is,

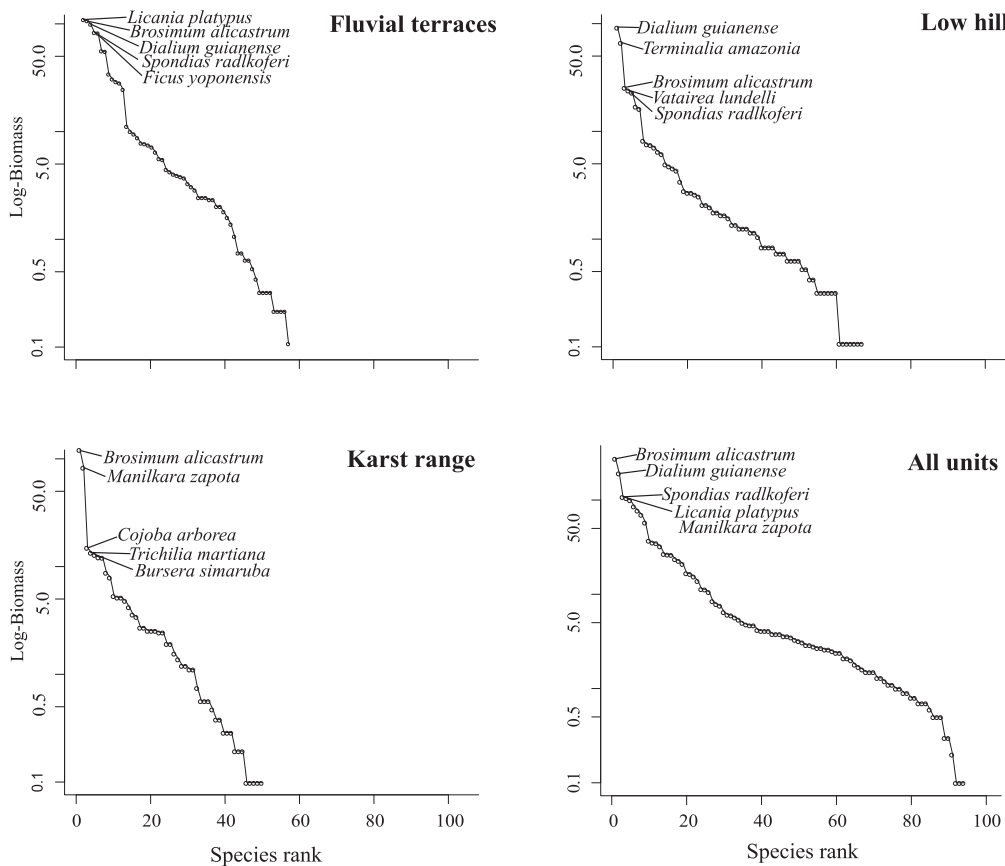


Fig. 3. Species-rank curves based on species aboveground biomass for tree assemblages supplying PFP in the Lacandon tropical rainforest, southeastern Mexico. Curves correspond to each of the three study landscape units (fluvial terraces, karst-range, and low hills) and to all sites combined (all units). On the X-axis, species are ranked in a decreasing order of biomass while on the Y-axis the logarithm of biomass (Mg) per hectare is indicated for each tree species.

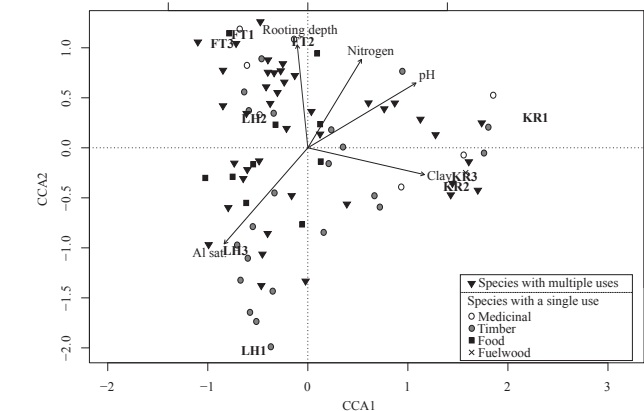


Fig. 4. CCA Bi-plot showing changes in the composition of species with PFPs across landscape units differing in soil and topography, as well as in the number and type of potential forest products in the Lacandon tropical rainforest, southeastern Mexico. Al sat. = aluminum saturation, FT = Fluvial Terraces, LH = Low Hills and KR = Karst Range. The symbols distinguish species with only one forest product category from species with multiple-uses.

therefore, an important step in designing appropriate integrated management and conservation programs for forest products, especially in heterogeneous TRF landscapes.

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Appendices A and B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.08.037>.

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